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The breeding of Spotted and Black Leopards

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(With two text-figures)

The black form of the leopard is shown to be inherited as an autosomal recessive to the spotted. The average size of litter from black females is smaller than that of the spotted. Neither the decline in average litter size with parity or age, the frequency distribution of litters per month, the number of litters per year and the sex ratio appears to differ between the black and spotted forms. Significantly more litters are born in the spring and summer months than in the autumn and winter months (Northern hemisphere data). The lower fecundity of the black form may be a factor in the maintenance of the black/spotted polymorphism of certain regions of Asia by opposing the yet unknown advantage possessed by the black morph.

INTRODUCTION

It is well known that the leopard may occur in two colour phases : the normal spotted and a black form. The latter is also known as the black panther. That the two colours belong to the same species is clearly shown by their identical morphology and the fact that they will inter-breed without difficulty. In certain areas of Asia (particularly in areas of extensive forest of Malaysia and Thailand), the spotted and black forms co-exist as a polymorphism (Pocock 1929, Tweedie & Harrison 1965). Genetically, this makes the melanic form of more than usual interest.

HEREDITY

Although it has been appreciated that the black form is the result of a colour mutation, precise information on the mode of inheritance is lacking. It is not necessary to seek far for the reason. Controlled breeding of leopards only occurs in zoos and few zoos could support a sustained breeding programme to determine the heredity. Also, the black form is more economically valuable than the spotted and cross-breeding is not usually undertaken unless a black mate cannot be found. However, despite these obstacles, it was decided that a circular among zoos known to be breeding leopards might produce sufficient data to resolve the problem. Accordingly, 128 zoos were circulated and, of these, 62 kindly made returns of their breeding experiences.

The breeding results obtained from the survey are shown in Table 1. Agreement between numbers of reported offspring and those expected are quite good and reveal that the black form is inherited as a monogenic recessive to spotted. It may be noted that the expected numbers for the first two entries do not fit those of ordinary Mendelian ratios and the reason for this resides in the nature of the data. Heterozygous animals capable of producing black offspring can only be detected by the occurrence of at least one black cub among their offspring. This means that sibships which do not contain black young will be excluded although of heterozygous parentage. Allowance has to be made for this in calculating the expectations. The sibship method of Fisher (1935) has been developed to deal with this situation and has been employed in the analysis. For the equivalent F_2 generation, the estimated frequency of the black gene is 37 per cent, a value which does not differ significantly from the expected 25 per cent ($\chi^2=2.0$). The estimate for the equivalent back-cross generation is 51 per cent, a value which scarcely differs from the expected 50 per cent ($\chi^2=0.33$).

The decisive results are the breeding of black cubs to spotted parents. This is conclusive evidence for recessive heredity of the black colour. Matings of black parents have given only black offspring. This is in full accord with expectation but the sheer weight of numbers observed is impressive. In addition to the data of the table, 20 matings of spotted \times black are reported in which only spotted progeny are produced. Ordinarily, these matings would not yield useful information but one sibship of 22 spotted young deserves mention. The result is very suggestive that black is recessive since, if it is not, this number of spotted young would be expected to occur by chance about once in 4×10^6 sibships of this size. This would be very long odds for the concept of dominance.

The complete absence of agouti hairs and the production of a uniform black phenotype is indicative that the leopard gene belongs to the general class of non-agouti mutants. It is proposed that the gene be designated

non-agouti and be symbolised as *a*. The non-agouti gene does not interfere with the development of the characteristic leopard spots or rosettes because this pigmentary system is independent of agouti. Thus, the spotted pattern can be discerned in the black form as a reflected pattern as the animal moves. It can also be photographically recorded by the use of flash photography.

TABLE 1

THE BREEDING OF SPOTTED AND BLACK LEOPARDS IN ZOOS OF THE WORLD

Parents	Offspring observed		Offspring expected	
	Spotted	Black	Spotted	Black
Spotted × Spotted ..	21	10	23	8
Spotted × Black ..	28	24	26	26
Black × Black ..	—	298	—	298

REPRODUCTION

Some interesting information on reproduction also became available as part of the survey. The average litter size for the leopard is usually taken to be two cubs and this is borne out by the data (Table 2). Rather surprisingly, however, when the litters are partitioned according to the colour of the mother, the black females do not appear to have so many young on the average as the spotted. The difference of means (0.39 ± 0.09) is statistically significant.

Interpretation of the difference is not easy. The simplest explanation is that the black female is not so fecund as the spotted. This may be the case. However, it is wise to be aware of other factors. For instance, foetal degeneration is a constant feature of mammalian reproductive physiology and the observed results could arise if the black form is slightly less viable than the spotted. That is, there is a small selective loss of black foetuses. Against this suggestion is the fact that the number of black cubs is not significantly below expectation as shown by Table 1. However, the number of cubs may not be large enough to detect the small difference involved. Another factor is the unavoidable loss of cubs which occurs between birth and the opportunity to record the colour. The number of such losses are small and there is no indication these are selective.

Once puberty has been attained, leopards will continue to have litters for a large number of years. The data is admittedly incomplete on this

TABLE 2

FREQUENCIES OF LITTER SIZES FOR SPOTTED AND BLACK FEMALE LEOPARDS

Female	No. in litter				No. of litters	Mean \pm S.E.
	1	2	3	4		
Spotted	37	89	38	7	171	2.09 \pm 0.06
Black	64	78	57	0	159	1.70 \pm 0.06

aspect of reproduction but that to hand is shown by Fig. 1. The curves in the figure represent averages of not less than 10 litters per consecutive litter. This had meant some grouping for the higher litter numbers. If this is not done, the graph becomes very erratic due to the small numbers involved (this can be seen for the curve for the spotted females, particularly). Two features are revealed by the figure, the first is the smaller average litter for the black mother in comparison with the spotted and the second is an apparent inherent downward trend. The curve for spotted females behaves erratically for high litter numbers, for the reason mentioned above, but that for black females is more steady and the larger numbers involved tended to stabilise the curve for the total. The decline could be ascribed to an effect of the non-agouti gene but this seems doubtful. The effect is probably due to a fall in fecundity with age, the effect being small at first but increasing progressively.

The distribution of births of litters for zoos in the northern hemisphere throughout the year is indicated by Figure 2. Apparently, there is no difference between the behaviour of the spotted versus black females for the 12-month cycle. However, for both forms there is noticeable seasonal variation. Though some reproductive activity is occurring throughout the year, more litters are born in the spring and summer months than in the autumn and winter months. The frequency distribution of births departs significantly from the simple assumption of uniform occurrence of litters over the twelve months ($\chi^2=20.1$ for 11 degrees of freedom). If a comparison is made for spring and summer months versus autumn and winter months, the significance is greatly increased ($\chi^2=21.1$ for 1 degree of freedom).

The frequency of litters per year per female differs considerably. A few females seem to have litters very irregularly; although the majority appear to have at least one litter per year, even if these are not always reared successfully. However, a fair number seem to have only one, rarely two, as if the reproductive cycle extends slightly beyond twelve

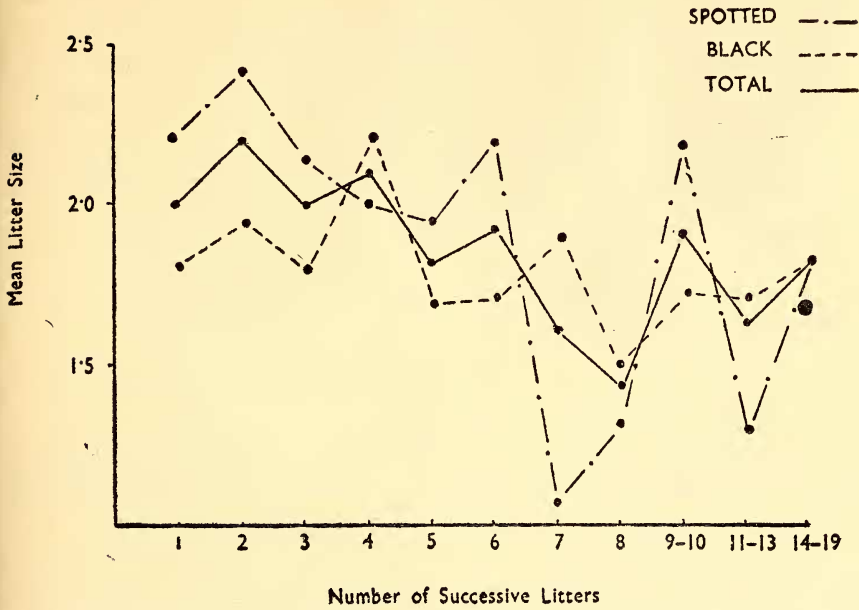


Fig. 1. The trend in mean litter size with successive parities.

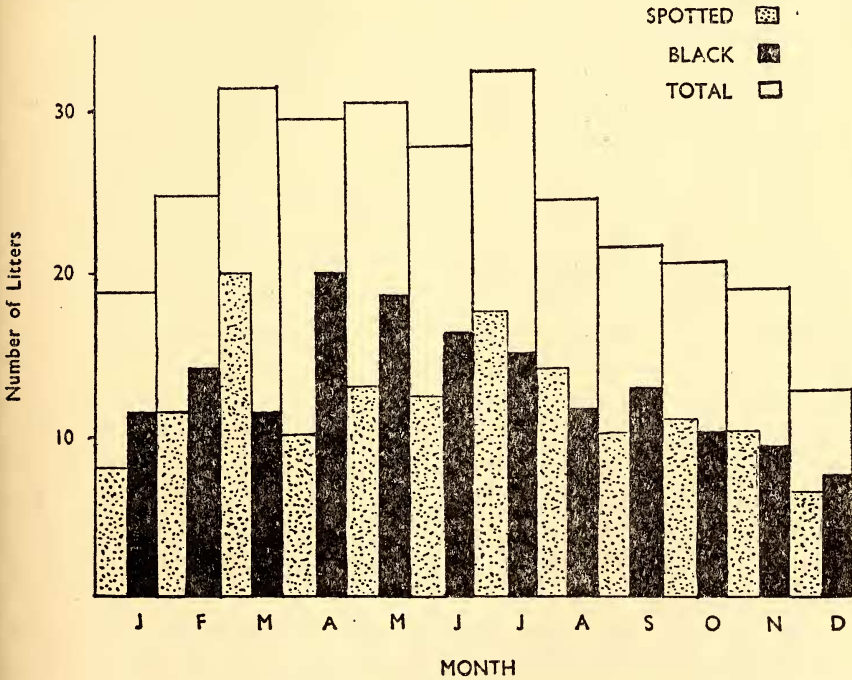


Fig. 2. Distribution of litters throughout the year.

months. Still others, on the other hand, manage two litters per year, with an occasional lapse of one litter per year. This variation, of course, could reflect the environment (housing, diet) in which the animals are kept as much as the innate reproductive rhythm. For instance, it is possible to secure three litters within or just over a year if the young are fostered or hand reared immediately after birth.

The sex ratio does not differ between the spotted and black forms. For 147 spotted animals, the ratio is 113 : 100 of males and females, for 195 black animals, the ratio is 110 : 100. The overall ratio is 111 : 100. This ratio does not differ significantly from equality of the sexes but, nevertheless, would be quite in accord with the general mammalian sex ratio of a small excess of males.

DISCUSSION

Hitherto, there have been differences of opinion whether or not the black form is inherited as a dominant or recessive. Gee (1948) proposed recessive heredity although his data (in keeping with most other) could not establish this unequivocally. However, the problem has now been resolved and it may be conjectured whether the result has any significance for the nature of black variants in other felids. It is not unreasonable to assume that the majority of these black forms are the outcome of single gene mutations. The difficulty is that of deciding upon the mode of inheritance.

Black forms are known to occur in the jaguar, lynx, puma, serval, Temminck's golden cat and tiger (Ulner 1941) and potentially for all other wild felids. The heredity of the black colour will presumably be an enigma until the chance observation of the birth of a black cub from two wild coloured parents or a wild coloured cub from black parents. Yet, can any information be obtained from a minute examination of the black phenotype? Provisionally, yes, for the following proposition may be advanced: when a black animal fails to show any agouti hairs (especially, on the head region, low down on the flanks or on the stomach), the form could be inherited as a recessive. It is true that some recessive black possess yellow hairs (*e.g.* house mouse), but these are restricted to specified areas and emerge under the microscope as all-yellow not banded agouti hairs. Any inference based on phenotype must of necessity be regarded as tentative and be subject to confirmation or otherwise at the earliest possible moment by breeding data. The proposition might not be worth making but for the extreme difficulty of securing breeding data for wild felids.

The spotted or striped pattern so characteristic of most felids is a pigmentary system independent of agouti and displays variation. Frequently, this is in the direction of greater melanism, where spots or ros-

ettes fuse to form stripes or stripes to form blotches. Ulner (1941) has described a leopard in which the spots coalesced to produce stripes on the back. In this sort of melanism, agouti coloration is persistent even if reduced in amount, hence there is no question of recessive non-agouti inheritance. In the domestic cat, the blotched *catus* pattern is inherited as a recessive to the striped wild type *silvestris* (Robinson 1959). However, it would be unwise to deduce too much from this. Unlike non-agouti, which occurs in many species and invariably behaves as a recessive, the *catus* type melanism of the cat is the only analysed case of its kind.

The apparent lower fecundity of the black form invites comparison with the persistence of the spotted/black polymorphism of the leopard in parts of south-east Asia. If the disadvantage also operates in the wild, it is tempting to suppose that it may be a factor in the maintenance of the polymorphism. The black form has an evident advantage over the spotted, otherwise it would not be so persistent. Polymorphisms exist because of the inter-play of balancing opposing selective forces. The leopard case could be of the simplest kind, of course, such as the influx of dominant spotted genes from outlying areas where the black phenotype has no advantage. On the other hand, the polymorphism could be more complex and the infecundity could be one of the negative factors involved. If the situation is complex, the failure of the black form to completely displace the spotted could hinge on the infecundity. Unfortunately, little is known of the totality of factors which contribute towards the polymorphism. Among the positive factors, greater concealment is a facile possibility but experimental verification of this in the field would be desirable.

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